EFFECTS OF A BIOCONTROL AGENT ON FORAGING BEHAVIOR IN THE BLACK-CAPPED CHICKADEE POECILE ATRACAPILLUS AND MOUNTAIN CHICKADEE POECILE GAMBELI

Effects of a biocontrol agent on foraging behavior in the Black-capped Chickadee *Poecile*

atracapillus and Mountain Chickadee *Poecile gambeli*

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Introduction

The control of invasive species by their natural enemies is an attractive and theoretically reasonable solution for controlling some invaders. The Enemy Release Hypothesis theorizes that invaders benefit from having escaped their native pathogens, parasites and predators as part of their movement and establishment into a new range (Keane & Crawley 2002; Torchin et al. 2003). This hypothesis suggests that releasing natural enemies, called biological control agents, can establish top-down control and effectively manage invasive populations (Bellows 2001, Cory & Myers 2000). Unfortunately, biological control (also know as biocontrol) agents can and do have unintended consequences both directly through such mechanisms as host shifting and indirectly through complex interactions with community structures and food webs (Louda et al. 1997, Simberloff and Stiling 1996, Pearson and Callaway 2003). In western Montana, 13 species of biocontrol insects (representing moths, weevils, and flies) have been released in an attempt to control spotted knapweed *Centaurea maculosa* (Lang et al. 2000). Several of these biocontrol agents have established, spread, and become numerous throughout spotted knapweed infestations in western Montana. In particular, the seedhead gallflies *Urophora affinis* and *U. quadrifasciata* have been very successful colonizers of spotted knapweed throughout its invaded range without becoming very effective biocontrol agents (Story et al. 1987).

The indirect effects of *Urophora* larvae on the native, omnivorous deer mouse *Peromyscus maniculatus* have been well documented. Deer mice consume *Urophora* larvae in quantities exceeding 800 larvae per mouse/night (Pearson et al 2000), leading to an increase in mouse density and overwinter survivorship (Ortega et al 2004, Pearson and Callaway 2006, Pearson and Fletcher 2008). The seasonal availability of *Urophora* larvae has been shown to cause shifts in microhabit use in deer mice, increasing the zone of influence of this exotic food subsidy (Pearson et al. 2000). The deer mouse is able to take advantage of this food subsidy because, as a generalist, it has plastic behaviors and broad dietary requirements. The ability to dramatically shift diet and microhabitat allows deer mice to exploit *Urophora* while co-occurring small mammals such as the meadow vole *Microtus pennsylvanicus,* which has a more specialized diet, consume less than two percent of observed capitula in knapweed infested areas (Story et

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al 1995, Lindroth and Batzli 1984). In addition, gallfly subsidies to deer mice have altered its status as a reservoir for Sin Nombre virus, leading to an increase in hantavirus incidence in mouse populations living in knapweed/*Urophora* infestations (Pearson and Callaway 2006).

Another small, omnivorous native organism has been documented preying upon *Urophora* larvae in the winter months: the Black-capped Chickadee *Poecile atracapillus* (Story et al 1995). Story 1995 documented Black-capped Chickadees in a knapweed/*Urophora* infested area using as much as 65% of their foraging time budget to prey on *Urophora* larvae within knapweed seedheads. Mountain Chickadees (*Poecile gambeli*) have also been observed foraging on gall-fly larvae (pers comm), but the research area investigated by Story et al. (1995) did not have Mountain Chickadees as part of the overwintering passerine community, so little is know about the degree to which this species utilizes gallfly larvae. However, given that these species often develop mixed foraging flocks during winter months in habitats invaded by spotted knapweed, there is potential for this novel biocontrol food resource to affect individual species' biologies and interspecific interactions.

Black-capped Chickadees do not survive under food scarce conditions for more than 48 hours in extremely cold weather, and overwintering Black-capped Chickadees only store limited amounts of fat; enough to survive a single average winter day without foraging (Smith 1991, Brittingham and Temple 1988). The Mountain Chickadee has similar habits, energy needs and morphology to the Black-capped Chickadee, although it has a more specialized diet (Smith 1991). The ranges of the two species can overlap in large areas during the winter and spring months as the Mountain Chickadees travel to lower altitudes and join mixed flocks with Black-capped Chickadees, Red-breasted Nuthatches *Sitta canadensis*, Pygmy Nuthatches *Sitta pygmaea*, and other common overwintering passerines. These mixed flocks are thought to confer advantages to their members via increased vigilance for predators, greater foraging efficiency, and a decrease in agonistic intraspecies interactions (Morse 1970, Barash 1974). Studies of Black-capped Chickadees have shown that supplemental feeding increases over-winter survivorship, decreases fat loading, and increases foraging behaviors during extreme cold events (Brittingham and Temple 1988). Interestingly, studies have also shown that Black-capped Chickadees

have higher survivorship, higher numbers of fledglings, and greater definition of territory boundaries in unaltered habitats (Fort and Otter 2004a, 2004b). Thus, it is not entirely clear what, influence *Urophora* may have on the two species of chickadees living in close proximity to dense infestations of this winter and spring food resource. These infestations present a unique combination of increased food availability, novel resource distribution, and are associated with significant habitat disturbance. The influence of *Urophora* on these two chickadee species in western Montana presents an interesting case study in the effects of biocontrol release on two native passerines; the Black-capped and Mountain Chickadees.

Objectives

This two-year study sought to quantify the effects knapweed and *Urophora* infested fields have on chickadee foraging and behavioral ecology. A year in the life of a chickadee can be roughly divided into two behaviors based on the time of year; social flocking (autumn through early spring) and breeding (mid spring through summer) (Odum 1942). During the social flocking period, I compared: 1) foraging incidences and distance from cover to access different prey items, 2) individual chickadee food preferences, and 3) behaviors that varied between gender, species, or individuals.

Methods

Three field sites were located such that each field site consisted of a matrix of open spaces invaded by knapweed and coniferous native forest and a single mixed flock of over-wintering passerines. Two of these sites were near the Bitterroot River (elevation 945m) and dominated by ponderosa pine *Pinus ponderosa*. The third site was a highly disturbed dry upland habitat (elevation 1220m) with a mixed tree community consisting of ponderosa pine, Douglas-fir *Pseudotsuga menziesii*, and sub-alpine fir *Abies lasiocarpa*. Each field site had a varying density of knapweed as the understory or the primary cover (from 0% cover to >80% cover). The remaining native understory largely consists of bluebunch wheatgrass *Psuedoroegnaria spicatum*, Idaho fescue *Festuca idahoensis*, yarrow *Achillea millefolium,* red osier dogwood *Cornus sericea*, and pacific ninebark *Physocarpus capitatus*. Each field site had trails,

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roads, and other human disturbances that habituated the chickadees to frequent, benign human presence. All field sites were located at least 1 km from human habitation to decrease the chances that chickadees used backyard feeders during the study period.

Intensive trapping efforts were initiated in early winter 2005/2006. Entire focal flocks were netted in 2005/6 and 2006/7 (to the best of our ability) in multiple days using chickadee mobbing call playback alongside taxidermy mounted predators (Great-horned Owl *Bubo virginianus* and Northern Saw-whet Owl *Aegolius acadicus*) to lure the flocks into a mist net. Trapping took place between 900 and 1200 hrs during relatively wind-free days to decrease the visibility of mist nets. We did not trap on days with more than trace precipitation or when the temperature was below -12° C. Trapped birds were promptly removed from mist nets once interest in the lures waned and the chance of catching additional birds was low, which was typically 5 to 10 minutes of sustained mobbing. Each bird was banded with a USFWS aluminum band and three color bands, forming a unique pattern. The birds also had a small blood sample taken from the brachial vein to allow chromosomal sexing at a later date, and a small breast feather sample taken as a back-up to the blood sampling. Observations of dominance behavior, as well as early spring mating behaviors, will be used alongside the chromosomal sexing to construct the basic hierarchy of birds in focal flocks. Gender, and therefore dominance, information will be used to evaluate differences between dominant and subordinate birds in *Urophora* foraging locations and proportions of *Urophora* larvae in their diets. All methods have been approved by University of Montana Institutional Animal Care and Use Committee (IACUCs 009-06RCDBS-022406 and 1009-06RCDBS-022406). At the completion of each trapping session at each site, we estimated numbers of birds in a given flock that went uncaptured.

Each focal flock of birds was observed through binoculars throughout the winter and spring of 2005-2006 and 2006-2007. We recorded observations on: feeding behaviors, food items consumed (if clearly seen or determined via chickadee food handling behaviors), dominance behaviors (intentionally displacing another bird or coming into physical contact with another bird), perching substrate by plant species including part of substrate (i.e. branch or trunk) and distance from the edge of cover if within cover or distance from cover if exposed, general knapweed density within a 5 m radius, bird height, and

weather. Observations of each chickadee also included its unique color band (if applicable) other marked/unmarked chickadee presence, and any distinct vocalizations that were be positively assigned to that individual.

All observations took place between 0800 and 1700 hrs. Foraging observations on individuals were limited to four consecutive 30-second interval observations on a single bird each time. For each individual observed, once the four (or less) observations were complete, a new individual in the flock was selected and observed. This aided in ensuring that the bias towards observing birds performing more conspicuous behaviors was minimized and increased the chance that birds with more cryptic behavior patterns (such as remaining near the trunks of densely needled trees) were included in the observations. Due to the smaller number of Mountain Chickadees in mixed flocks (typically a 1:4 ratio of Mountain Chickadees to Black-capped Chickadees) the Mountain Chickadee data was not as numerous or complete as for Black-capped Chickadees. Chickadees were selected at random within the mixed species flocks for two minute observations, and thus Mountain Chickadees were observed in rough proportion to their abundance. Above 12 m ht, color banded chickadees were very difficult to identify and it was difficult to maintain visual contact with birds. Therefore data from >12 m ht is less robust.

Results

The difference between the food choices of Black-capped Chickadees and Mountain Chickadees were quite stark. When in mixed flocks, marked Black-capped Chickadees consumed gallflies for 44%, and other (presumed native) invertebrate prey for 48% of their observable foraging. Mountain Chickadees only consumed gallflies for 14% of observed foraging incidents, and consumed other invertebrates for 74% of their foraging. The rest of the diet of both chickadee species was nuts, seeds and berries, making up 7% and 11%, respectively, of what the birds were observed consuming.

The behaviors used by the two chickadee species to access the gallflies were very different. Observable behaviors were assigned to four categories; hawk (to hover and pluck a seedhead from a standing knapweed stalk), stem (to fully land on a knapweed stem and pluck a seedhead), ground (to find

and take a seedhead from the ground by hopping around or landing in a predetermined area), and other (typically landing on an alternate substrate, like a barbed wire fence strand or a rock). Black-capped Chickadees preferred to hawk (51%) or stem (32.5%) the seedheads, and occasionally were seen using the ground technique (8.5%) or other (8%). Mountain Chickadees overwhelmingly preferred the ground technique (80%) and used the hawk (4%), stem (8%) and other (8%) rarely. In nearly all cases, the individual bird used one of these techniques to snap or grab the seedhead *in situ*, but then retreated to a covered perching location, typically the interior of a ponderosa pine, to actually consume the gallfly larvae.

The distribution of foraging behaviors of Black-capped Chickadees when harvesting knapweed seedheads closely mimics the distribution of observed foraging behaviors for native invertebrate food sources (Fig. 1). When clumped into two groups, three of the four categories can be re-classified into non-ground based feeding (hawk or stem) and ground based (ground). For Black-capped Chickadees, this results in knapweed seedhead gathering having a ground to non-ground ratio of 1:10.7, while native invertebrate foraging has a similar ratio of 1:6.5.

In contrast, Mountain Chickadee foraging ratios for ground or non-ground based prey did not trend towards the same direction (Fig. 2). The ratios do not follow the same basic pattern when divided by food type; with knapweed seedhead gathering, the ground to non-ground ratio was 1:0.25, and native invertebrate foraging was 1:3.8.

For Black-capped Chickadees, the distance traveled from cover to access a food resource varied according to food type (Fig. 3). The most common distance in all three food categories was 0 m, with an overwhelming majority of recorded foraging incidents of native invertebrates and seeds (94% and 93%) being accessed while under cover of a shrub or tree. For knapweed seedheads, 68% of recorded foraging incidents took place under cover, while a notable 20% took place 0.1-1.5 m from cover, and 12% took place ≥2 m from trees and shrubs.

Black-capped Chickadees did not, however, process and consume foods at significantly different distances from cover according to type of food. In fact, when compared across food types, no differences

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in distance from cover for processing location were found. Therefore, Black-capped Chickadees who accessed a food resource, near or far from cover, were equally likely to fly to a covered location to consume it- without regard to the original location of the food item.

As a group, Black-capped Chickadees were observed foraging for gallflies for 45% of incidents, native invertebrates for 48%, and seeds or nuts for 7%. However, individual birds did not necessarily adhere to this distribution. Variation within the species was significant, with some frequently observed individual birds strongly preferring gallflies, others falling into the center of the distribution, and some strongly preferring native invertebrates. Due to the relatively lower number of individual Mountain Chickadees marked and observed, as well as the difficulty in locating them on a consistent basis, the data for individual Mountain Chickadees is not sufficient to draw strong conclusions.

Discussion

Black-capped Chickadees and Mountain Chickadees both consumed seedhead gallfly larvae throughout the social flocking period. Both species could be observed using a variety of techniques to harvest seedheads. However, a number of differences can be clearly seen.

Black-capped Chickadees were observed successfully foraging for seedhead gallfly larvae more than they were seen foraging for native invertebrates or for plant foods (seeds, fruits and nuts). This species regularly consumes a diverse diet, allowing it to exploit this relatively new food source in its environment. On the other hand, the Mountain Chickadee has a fairly constricted typical diet, with a much higher level of specialization. Potentially as a result of this pre-existing lack of diet plasticity, and despite being in the same mixed flocks and thus same habitat as the Black-capped Chickadees, the Mountain chickadees averaged a rather small percentage of their observed foraging incidents occurring on seedhead gallflies.

The difference in the behaviors of Black-capped Chickadees and Mountain Chickadees in the moment of seedhead access was quite striking. Extremely few Mountain Chickadees were observed using the "hawk" or "stem" behaviors to collect a seedhead, while these were the predominant methods used by

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the Black-capped Chickadees. Small differences in morphology by these congeners naturally exist, so it is theoretically possible that the acrobatics that permit a Black-capped Chickadee to snatch a seedhead off a plant while hovering above the plant are extremely challenging for a Mountain Chickadee's muscular structure or wing loading. It is also possible that the wider scope and variety of native foods that the Black-capped Chickadees use have led to a far greater inventiveness in the species in terms of food accessing behaviors. Incidental to the study, Black-capped Chickadees were also observed landing on mullein (*Verbascum thapsus*) stalks, arrowleaf balsamroot (*Balsamorhiza sagittata*) stalks, red-osier dogwood (*Cornus sericea*) stems, and other unstable perches while consuming small invertebrates from the tips- a behavior very similar to the hover and snatch behaviors needed to access a knapweed seedhead from a standing plant. Mountain chickadees were not observed performing these more acrobatic behaviors.

The tit family (*Paridae*), as a whole, is known for its unusual ability to learn how to access new food resources (Fisher and Hinde 1949). While knapweed seedhead gallflies are certainly not as novel a food item as a bottle of cow's milk on a London doorstep, it is still a non-native invasive plant that contains a well-hidden non-native insect larvae. My results show that Black-capped Chickadees have learned to access this food resource quickly and efficiently, while using behaviors that are thought to minimize the amount of time spent out from under cover and potentially exposed to predators. However, the Mountain Chickadee has not. The data show them only using this food source as a small component of their foraging budget, and they are generally accessing it while hopping about on the ground, looking directly down. This ground-based foraging is thought to represent a more risky behavior strategy. Mountain Chickadees spend a very small minority of their time foraging on the ground for native sources of food, which makes it all the more interesting that the method they predominately use to collect knapweed seedheads is to hop around on the forest floor.

It may be that the difficulties that Mountain Chickadees seem to have in collecting seedheads quickly and safely, whether due to physical (wing loading) or behavioral (failure to socially learn)

limitations, is constraining Mountain Chickadees exploitation of this novel resource. It could also be driven by other factors. The lack of need or desire to diversify the daily diet of a Mountain Chickadee may mean the inventiveness and agility shown by the Black-capped Chickadees is just unnecessary. Whatever the underlying reason, the differences in the foraging incident percentages, and behaviors observed, are quite significant. Despite these birds being the same genus, spending the winter in the same social flocking groups, and having very similar basic behaviors and anatomy, the ways in which they exploit seedhead gallfly larvae as a food resource are quite divergent

Chickadees are vulnerable to aerial predators such as Northern Pygmy Owls and smaller accipters (Templeton et al. 2005). Both Black-capped and Mountain Chickadees were rarely observed outside of cover (consisting of tree or shrub branches) for more than a brief moment. It is therefore quite important to note that knapweed densities decrease under covered or shady areas, and increase in open areas. Both species of chickadees very rarely remained outside of cover after a seedhead was collected in their beak. Instead, an individual chickadee would retreat to the nearest convenient covered location-typically a low branch of a ponderosa pine. This behavior of darting out into the open, collecting a seedhead, and then darting back into the tree was not seen as frequently when chickadees were collecting native foods. As a result of the distribution of knapweed, and therefore of seedhead gallfly larvae, chickadees are exposing themselves to a situation with greater risk from aerial predators than they normally experience when collecting native foods. It is possible that this increase in time spent in open areas results in differences in mortality rates from those mixed flocks that do not spend time in knapweed infested forest-field matrixes.

On the other hand, since winter food resource availability greatly enhances chickadee over-winter survival, chickadees accessing gallflies may experience greater over-winter survival and increased population densities compared with chickadees lacking access to this novel and superabundant food resource. As shown by previous work for species such as deer mice, such food subsidies can have significant ramifications not only for the recipient species populations but also for other community members through indirect interactions (Pearson and Callaway 2003, 2006, 2008). The current study

expands on prior work by examining how behavioral plasticity may allow some species to benefit from novel conditions associated with exotic species while other less flexible species may gain little or even be negatively impacted (*sensu* Pearson 2009).

Biological control organisms that colonize their host plant, but then fail to significantly decrease the population, can become present in the landscape at very high densities. In the case of the seedhead gallfly, this high density of a potential prey species for native omnivorous species like mice and chickadees has proven to alter natural foraging patterns. Whether or not the chickadees are experiencing net benefits in fitness from this new food resource is not needed to infer that biological control, in this instance, has created a set of unintended consequences for two common native passerines.

References:

Barash, D.P. 1974. An Advantage of Winter Flocking in the Black-capped Chickadee, Parus Atricapillus. Ecology **55**:3: 674-676.

Brittingham, M.C., and S.A.Temple. 1988. Impacts of Supplemental Feeding on Survival Rates of Black-Capped Chickadees. Ecology **69**:581-589.

Chew, M.K. & Laubichler, M.D. 2003. Natural enemies – metaphor or misconception? Science 301:52–53.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac H.J. 2004 Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721–733

Denoth, M., Frid, L. & Myers, J.H. 2002. Multiple agents in biological control: improving the odds? Biol. Con., 24, 20–30.

Ekman, J.B. and K. Lilliendahl. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. Behavioral Ecology 4:232-238

Fisher, J. and R. A. Hinde. 1949. The opening of milk bottles by birds. British Birds **42**:347–357.

Fort, K.T. and K.A. Otter. 2004a. Effects of Habitat Disturbance on Reproduction in Black-capped Chickadees (*Poecile atricapillus*) in Northern British Columbia. Auk **121**:1070-1080

Fort, K.T. and K.A. Otter. 2004b. Territorial breakdown of Black-capped Chickadees, *Poecile atricapillus*,in disturbed habitats? Animal Behaviour **68**:407-415

Keane, R.M. & Crawley, M.J. 2002 Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol., 17, 164–170.

Lang, R.F., Richard, R.D., Parker, P.E., Wendel, L. 2000. Release and establishment of diffuse and knapweed biocontrol agents by USDA, APHIS, PPQ, in the United States. Pan-Pac. Entomology **76**, 197-218.

Lima, S.L. and P.A. Bednekoff. 1999. Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. American Naturalist **153**:649-659

Lindroth, R.L. Batxzli, G.O. 1984 Food Habits of the Meadow Vole (Microtus pennsylvanicus) in Bluegrass and Prairie Habitats. J Mammology 65:600

Louda, S. M., Kendall, D., Connor, J., Simberloff, D. 1997 Ecological Effects of an Insect Introduced for the Biological Control of Weeds. Science 277:1088-1090

McFayden, R.E. 1998 Biological Control of Weeds. Ann Rev Entomology 43:369-394

Morse, D.H. 1970. Ecological Aspects of Some Mixed-Species Foraging Flocks of Bird. Ecological Monographs **40**:119

Odum, E.P. 1942. Annual Cycle of the Black-capped Chickadee. Auk **59**:499-531

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Ortega, Y.K., D.E. Pearson and K.S. McKelvey. 2004. Effects of biological control agents and exotic plant invasion on deer mouse populations. Ecological Applications **14**:241-253

Pearson, D.E., K.S. McKelvey and L.F. Ruggiero 2000. Non-target effects of an introduced biocontrol agent on deer mouse ecology. Oecologia **122**:121-128

Pearson, D.E., and R.M. Callaway. 2003. Indirect effects of host-specific biological control agents. Trends in Ecology and Evolution. **18**:456-461

Pearson, D. E., and R. M. Callaway. 2005. Indirect nontarget effects of host-specific biological control agents: implications for biological control. *Biological Control* 35:288-298.

Pearson, D. E. and R. M. Callaway. 2006. Biological control agents elevate hantavirus by subsidizing mice. *Ecology Letters* 9:442-449.

Pearson, D. E. 2009. Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. Oecologia 159:549-558.

Saether, B.E., Bakke, O. 2000. Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. Ecology. **81**:642-653

Sheley, R.L., S.J. Jocobs and M.F. Capinelli. 1998. Distribution, biology and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technology **12**:353-362

Simberloff, D., and P. Stiling. 1996. Risk of Species Introduced for Biological Control. Biological Conservation **78**: 185-192

Story, J.M., R.M. Nowierski and K.W. Boggs. 1987. Distribution of *Urophora affinis* and *U. quadrifasciata*, two flies introduced for biological control of spotted knapweed (*Centaurea maculosa*) in Montana. Weed Science **35**:145-148

Story, J.M., K.W. Boggs, W.R. Good, L.J. White and R.M. Nowierski. 1995. Cause and extent of predation on *Urophora* spp. Larvae (Diptera: Tephritidae) in spotted knapweed seedheads. Environmental Entomology **24**:1467-1472

Templeton, C. N., E. Greene, K. Davis. 2005. Allometry of alarm calls: Black-capped Chickadees encode information about predator size. Science 308:1934-1937.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J. & Kuris, A.M. 2003. Introduced species and their missing parasites. Nature 421:628–630.
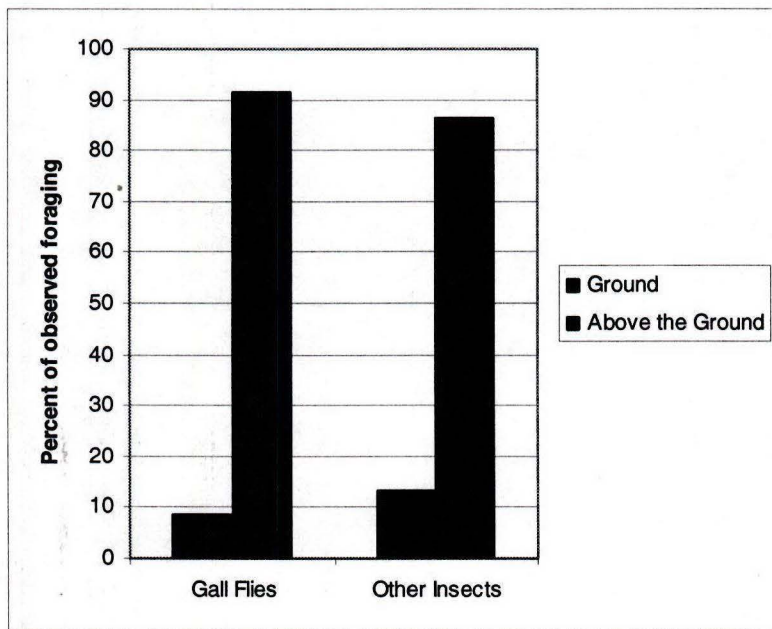
Figure 1. Black-capped Chickadee foraging event locations by prey type.
Black-capped Chickadees were observed foraging for prey on the ground or above the ground at very similar ratios for both seedhead gallfly larvae and natural insect prey.
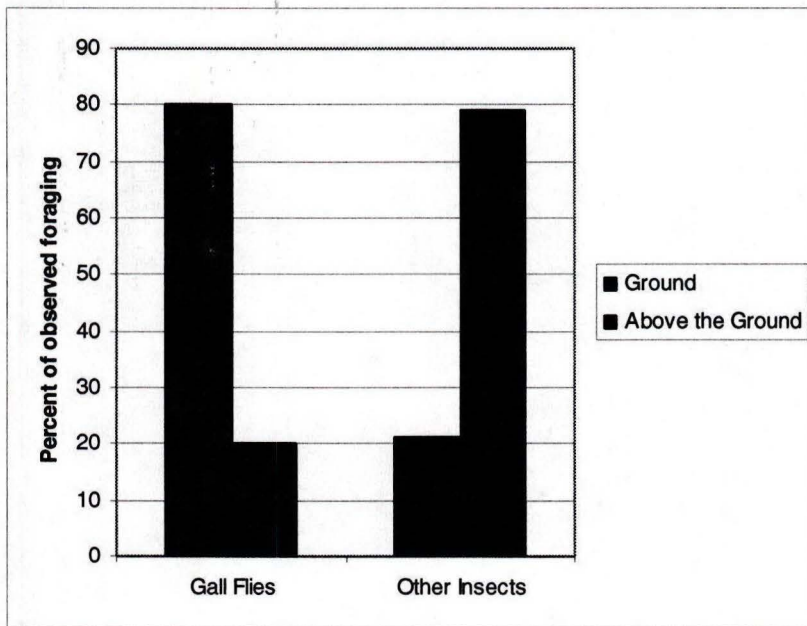
Figure 2. Mountain Chickadee foraging event locations by prey type. Mountain Chickadees were observed foraging for prey on the ground or above the ground in opposing manners depending on prey type, with seedhead gallfly larvae foraging events predominately taking place on the ground.
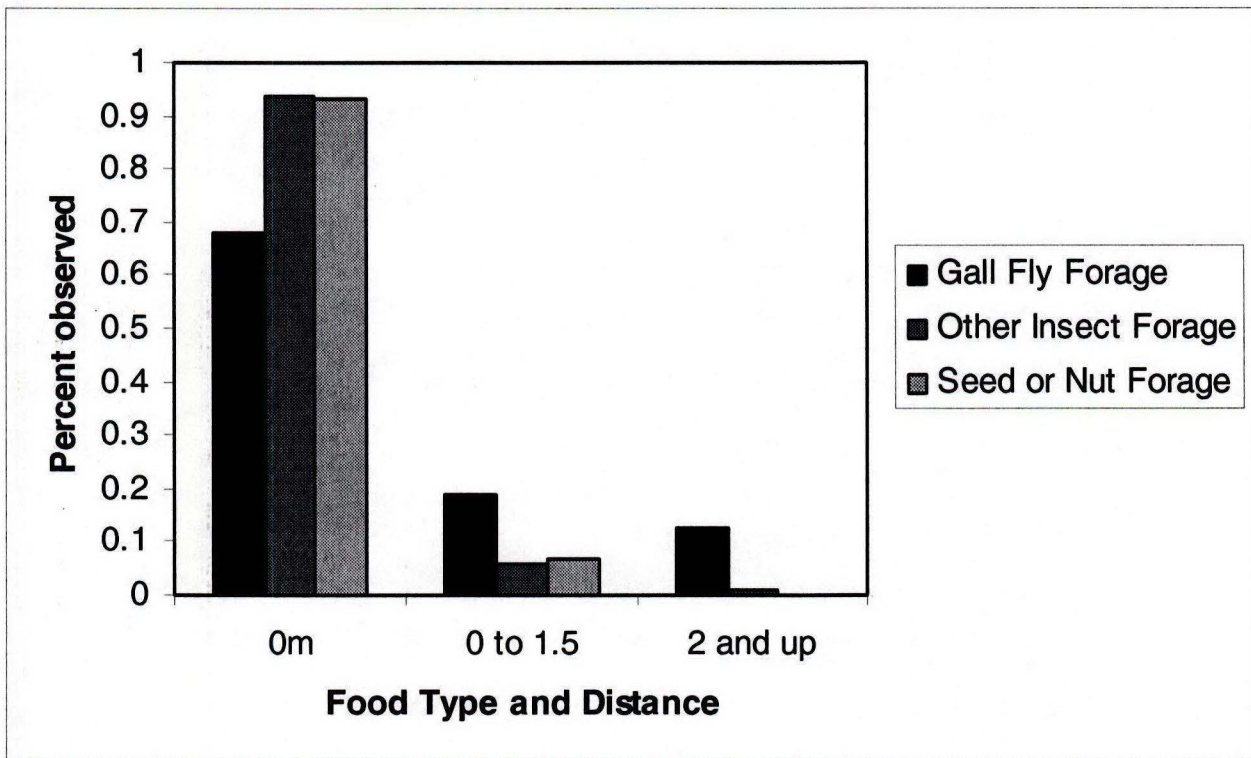
Figure 3. Distance in meters from foraging Black-capped Chickadee to cover by food category. Black-capped Chickadees traveled farther distances from cover to forage for seedhead gallfly larvae than when foraging for foods in the other categories (other insects, seeds or nuts).